Does management of a top carnivore influence the response of mesopredators and prey to rainfall in arid ecosystems? Evidence for a Baseline Density theory

Renee L. Brawata

Fenner School of Environment and Society, The Australian National University, Canberra ACT 0200, Australia.

Current address: Conservation Research, Environment, Planning and Sustainable Directorate, ACT Government, Mitchell ACT 2911, Australia.

Ph +61 2 6207 0636

Email: renee.brawata@act.gov.au

ABSTRACT

The removal of apex carnivores from ecosystems can impact the abundance and diversity of species in lower trophic levels. In arid ecosystems, where "bottom up" forces of primary productivity and resource availability strongly affect trophic interactions, the role of "top down" effects is still much debated. This study explored the potential role of an apex predator, the dingo, as a "top down" trophic regulator in Australian arid ecosystems under different levels of primary productivity and dingo management regimes. Consistent with the theory of top down regulation, strong relationships were found between dingo management, dingo activity and fox activity. Dingoes appeared to suppress fox activity where dingoes were uncontrolled or only opportunistically controlled. At sites where dingoes were absent or in low numbers, fox activity was higher, and this inverse relationship persisted regardless of rainfall. The activity of rabbits and small mammals was lower where dingoes were absent and fox activity was high, while the activity of macropods was higher in the absence of dingoes. Feral cat activity did not differ significantly between sites under different dingo management or between years. These results suggest that management of dingoes is a key determinant of fox activity and the activity of some prey under varying levels of productivity. Evidence from this research showed that while the strength of trophic regulation by dingoes may fluctuate, top down effects occurred both prior to and post significant rainfall events. Following this, top down regulation of fox populations during dry periods at sites where dingoes are retained may enable higher and more stable "baseline" densities of small vertebrates, from which a larger and more rapid rate of increase of these prey during the "boom" periods can occur. Understanding the relative strength and interactions of top down and bottom up forces in regulating populations, and under what ecological states the importance of each changes, is important for the long-term conservation of biodiversity in arid regions.

Key words: dingo, mesopredator release, trophic regulation, apex predator, baseline density

DOI: https://doi.org/10.7882/AZ.2021.007

Introduction

The arid and semi-arid regions of Australia are traditionally viewed as "bottom up" ecosystems, where trophic interactions are regulated primarily by productivity (Morton *et al.* 2011). Many species fluctuate dramatically in response to environmental variability and perturbations, of which the most significant is rainfall (Fensham *et al.* 2005). Related vegetative productivity is then a key determinant of the abundance and distribution of many herbivorous species and the predators that prey on them (Dickman *et al.* 1999; Fensham *et al.* 2005; Letnic *et al.* 2005; Haythornthwaite and Dickman 2006; Letnic and Dickman, 2006; Previtali *et al.* 2009).

Alternatively, "top down" regulation identifies that apex predators exert regulatory forces on smaller predators, limiting their density and range (Terborgh and Estes 2010; Feit and Letnic 2019). The removal or reduction of large carnivores from ecosystems may lead to 'mesopredator release' (Soulé *et al.* 1988), where smaller predators are able to increase to higher densities in the absence of top down control (Crooks and Soulé 1999). Under such circumstances, the abundance and diversity of prey species susceptible to mesopredator predation may be greatly reduced (Bruno and Cardinale 2008). Both top down and bottom up forces may be active in the arid ecosystems

Downloaded from http://meridian.allenpress.com/australian-zoologist/article-pdf/41/3/417/3125756/i0067-2238-41-3-417.pdf by guest on 13 March 2024

of Australia (Pianka 1978). While productivity may act as a primary driver in ecosystems, top down forces may be important under explicit environmental conditions (Holmgren *et al.* 2006; Greenville *et al.* 2014), with interactions varying temporally and spatially in strength (Letnic *et al.* 2005).

The dingo (*Canis familaris dingo*), as an apex carnivore, may play a role in limiting populations of two exotic mesopredators—the red fox (*Vulpes vulpes*) and feral cat (*Felis catus*)—in some Australian ecosystems (Johnson and VanDerWal 2009; Letnic *et al.* 2009a, b, 2010; Letnic and Koch 2010; Kennedy *et al.* 2011). Some studies have shown that, where dingoes persist, fox activity is reduced and small (< 35 g) native mammal species persist in higher abundance (Smith and Quin 1996; Johnson *et al.* 2007; Wallach *et al.* 2009; Letnic and Koch 2010). The decline of many native fauna species, particularly small to medium-sized mammals, has been primarily attributed to predation by foxes and feral cats (Burbidge and McKenzie 1989; Short and Smith 1994); therefore, retaining dingoes in ecosystems may assist in the conservation of native species highly vulnerable to fox and cat predation (Risbey *et al.* 2000; Burbidge and Manly 2002).

The role that productivity plays in varying the strength of interactions between dingoes, mesopredators and native prey is not well understood. As such, it is unclear as to whether dingoes are able to maintain suppressive effects on mesopredators with increases in prey abundance in response to rainfall and what the implications of these factors are for native prey populations in the long-term. This study examines how dingo management influenced population indices for dingoes, foxes, feral cats and selected native prey both prior to and post a significant rainfall event in arid Australia.

Methods

This study was conducted as an observational study (Altmann 1996) of uncontrolled events at five study sites in arid Australia which had differing dingo management regimes. The five study sites were located in New South Wales and South Australia and included the properties of Sturt National Park (-29° 12′, 141° 58′), Bollards Lagoon (-28° 58′, 140° 51′), Quinyambie Station (-30° 12′, 140° 58′), Mundowdna/Wilpoorina (-29° 43′, 138° 13′) and Finniss Springs (-29° 44′, 137° 30′) (Figure 1). All study sites were located within the desert climatic zone, where droughts are frequent, and rainfall is highly variable.

The study sites were located either side of the dingo barrier fence (DBF), a physical barrier that separates southern areas with no dingo populations (or only a few individuals), from areas which contain relatively stable dingo populations north of the fence (Figure 1). The following dingo management regimes were found at each of the study sites: Finniss Springs (no control for > 5 years); Quinyambie Station (opportunistic shooting); Bollards Lagoon (no control for > 2 years at first sampling, then resampling 18 months post control); Sturt National Park (no control) and Mundowdna/Wilpoorina (control using sporadic baiting and shooting).

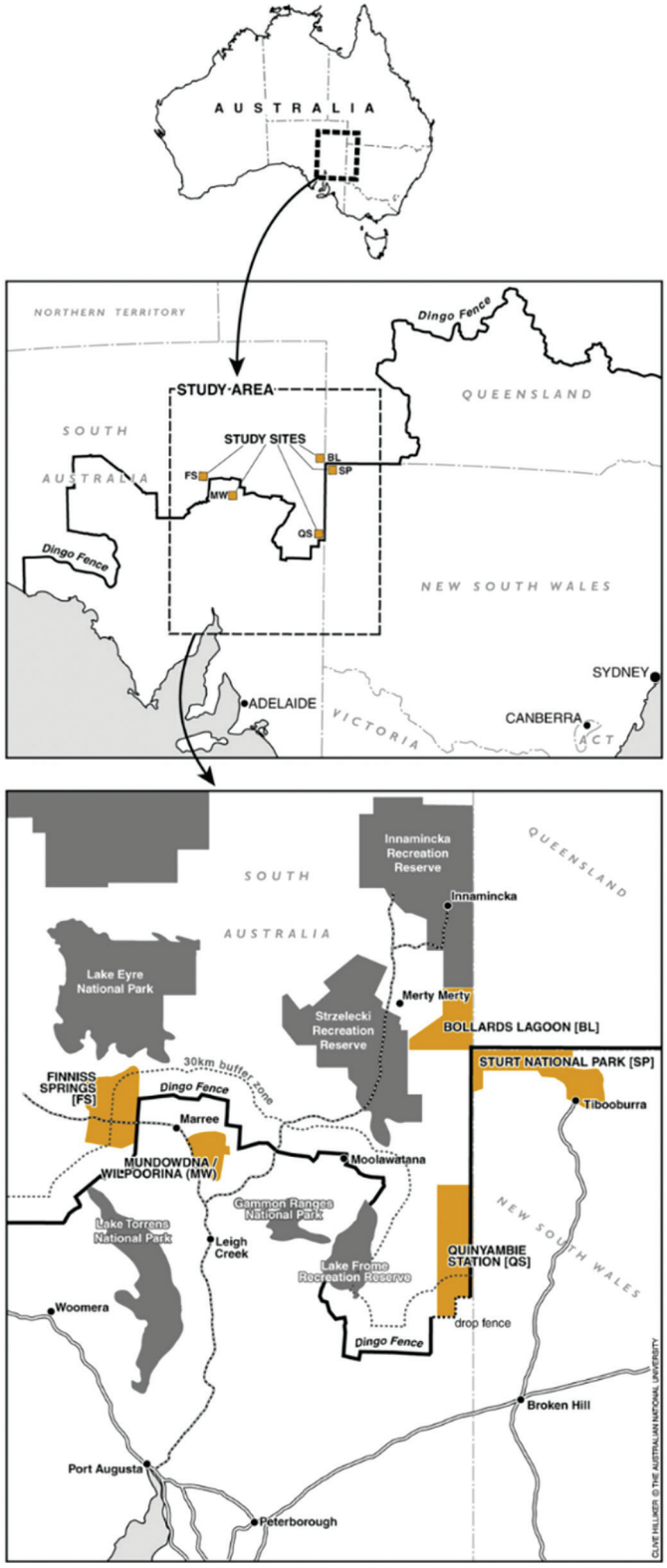

Figure 1. Map of the five study sites in arid Australia, showing their relative location to the Dingo Barrier Fence (DBF).

Downloaded from http://meridian.allenpress.com/australian-zoologist/article-pdf/41/3/417/3125756/i0067-2238-41-3-417.pdf by guest on 13 March 2024

Each study site was assessed for productivity. Gross primary productivity of each sampling area during the sampling period (GPP, mol CO_2 m^{-2} $month^{-1}$), as well as historical productivity (previous 7 years) (GPP, mol CO_2 m^{-2} $year^{-1}$) was used to estimate overall annual productivity. GPP was estimated using a continental remotely sensed time series database (Berry *et al.* 2007). Productivity peaks coincided most of the time for the five sites, with variations in the amount of productivity between sites. Sites located in sand dune country (Sturt National Park, Bollards Lagoon and Quinyambie Station) had higher productivity peaks and overall productivity than the two sites located in the salt lakes bioregion (Mundowdna/Wilpoorina and Finniss Springs).

The first sampling took place in 2006 (4 sites) after a number of years of low rainfall. A large rainfall event occurred across all sites 3 months prior to the 2007 sampling session (4 sites), with the final sampling session in 2008, one-year post rainfall (2 sites). Replication at each site was conducted on a spatial and temporal scale, with each site containing two separate sampling areas from which data were collected over two years. The two sampling areas at each site contained at least one major watering point and were separated by at least 10 km for sites north of DBF and by at least 3 km at sites south of the DBF. These distances took into account the radius of the average home range size of a dingo in the arid zone where artificial water is available (95.8 km^2) (Thomson 1992b; Thomson and Marsack 1992) and the average home range of a male fox (6.67 km^2) in the arid zone (Marlow 1992) as foxes were the species with the largest home range at sites south of the DBF. To limit seasonal variation within data, sampling took place only during the "summer" period (January–April).

Population indices for dingoes, foxes, feral cats and selected prey were estimated for each site. Prey categories included macropods, rabbits and other small vertebrate prey (small mammals and reptiles). These prey categories were chosen as they have been previously identified as a significant component of predator diets (Whitehouse 1977; Newsome *et al.* 1983a; Paltridge *et al.* 1997; Molsher *et al.* 2000; Read and Bowen 2001), were measurable using standard techniques, and were common at all five study sites.

Predator populations in this study were assessed using activity indices calculated from two methods of track counts: sand transects (passive track counts) and scent stations (active track counts). While the approach of using activity indices to estimate populations has limitations (Engeman *et al.* 2000), it is accepted that estimations of populations using activity indices enable researchers to compare temporal and spatial relative densities at the same site between years, or between sites. Prey activity was measured by sand transects and spotlighting.

The transect design and sampling method used in this study were based on findings by Mahon *et al.* (1998). In total, 15 transects per site were spaced randomly at a minimum distance of 400 m and a maximum of 3 km apart. Each transect measured 0.5 m wide and 50 m long and was located off roads so as not to bias sampling towards predator activity. Transects were checked once a day in the morning. All prints found were identified and categorised as either a predator species (cat, fox, dingo) or a prey category (rabbit, kangaroo, small mammal or reptile). Bird tracks and unknown tracks were discarded. Transects were checked on three consecutive mornings, the length of time previously determined as the optimal time for data collection using this method (Allen *et al.* 1996; Forsyth *et al.* 2005). The raw frequencies of tracks recorded (that is, the number of crossings per transect per day) were averaged over the number of days on which the transect was readable, and then standardised as the mean number of tracks / transect (50 m) per day (Allen *et al.* 1996). By summing up the counts over the total sampling days, problems associated with non-temporal independence of the samples were circumvented (Engeman *et al.* 1998; Edwards *et al.* 2000). Variance for the passive track counts was then calculated using the method outlined in Engeman *et al.* (1998).

A total of 20 scent stations per site provided a second, complementary estimation of predator activity in addition to transects. Scent stations were randomly placed a minimum of 400 m and a maximum of 3 km apart within a site. At each station, scent was applied to naturally occurring objects, such as bushes, rocks and sticks. The stations were "scented" with fox/dog and cat attractants including a mixture of prefabricated dog/fox scent (Feralmone, Pestat Pty Ltd, Bruce, ACT) and a food lure mixture (fish oil). Sand surrounding the stake was smoothed using a rake in a 1 m circumference to enable predator visitations to be monitored by recording prints left in the sand. Scent stations were checked for visitations on three consecutive mornings and the presence of each predator species was recorded. Visitations to scent stations were calculated as the total number of visitations for each species per total scent station exposures (total number of scent stations × number of sampling nights). Total counts were then averaged and standardised as the mean number of visitations/scent station/day. Sampling error variance was calculated from the ratio of visitations per scent station exposures.

Spotlighting was used to provide a second population index for large macropods (Arnold *et al.* 1994) and rabbits (Twigg *et al.* 1998; Ballinger and Morgan 2002; Poole *et al.* 2003). Spotlighting was conducted at night along vehicle tracks and commenced around one hour after sunset with an approximate duration of 2–3 hours. Two 20 km spotlighting transects were monitored over 3 nights at each sampling site. The spotlight was fixed on a standard distance setting so that a maximum observational strip of 100 m was seen either side of the road. Raw frequencies

Downloaded from http://meridian.allenpress.com/australian-zoologist/article-pdf/41/3/417/3125756/i0067-2238-41-3-417.pdf by guest on 13 March 2024

of prey species detected were standardised as the mean number of animals for each prey category (macropod and rabbit) per spotlight km, averaged over the three nights per transect. These means were then used to calculate the coefficients of variation between sampling areas.

The harvesting of macropods had to be considered for two study sites (Finniss Springs and Mundowdna/Wilpoorina) when interpreting results. At the time of the study, a professional shooter operated on Mundowdna/Wilpoorina, with a harvest quota of 1200 macropods per season (approximately 2400 annually). Indigenous harvesting of kangaroos was undertaken at Finniss Springs. No quantitative data on numbers of macropods harvested were obtained for either site, therefore the impacts of harvesting on macropod activity were considered qualitatively only.

A linear mixed model was used to calculate the mean PAI (Passive Activity Index; Allen *et al.* 1996) from transect data for each predator species and prey category at all study sites, using both site and year as fixed effects and night and sampling area as random effects (Engeman *et al.* 1998). Transect data for each species derived from the 20 transect plots per sampling area were pooled for each night (nights 1, 2 and 3). The effective sample size was used to estimate the standard error for each species.

Using binomially distributed data sets from scent stations (presence/absence of a species at an individual station each sampling night), a generalised linear mixed model, with site and year as fixed effects and sampling area and night as random effects, was used to calculate a linear predictor (η) for each species at each site per sampling year, so that:

$$pr(i,j) = \frac{1}{e^{-n_{ij}} + 1}$$

where pr is the modelled proportion of scent stations visited by a particular species at study site i for year j. A 95% confidence interval for each linear predictor was estimated ($\eta \pm t_{.975}$ (d.f. = 24) SE).

Observed visitation rates were then used to calculate the mean activity index for each predator species at a given study site per sampling night. A linear mixed model using study site and year as fixed effects, and sampling area and day as random effects, was used to examine the effects of study site and year on mean densities of dingoes, foxes and feral cats. The residual variation from this model was used to determine whether or not any clustering effects were present for each species per sampling night; clustering may arise from heterogeneity within predator populations.

Using spotlighting data, the total number of macropods and rabbits counted each night was divided by the number of kilometres driven, to provide an activity index for each prey species. The index was expressed as number of animals seen per spotlit kilometre each sampling night. These indices (n = 6) were then totalled over three nights of sampling at two sampling areas to estimate an average density index, standard error and coefficient of variation for each species per study site per year.

All analyses were conducted using the statistical software package GENSTAT (VSN International 2008).

Results

Predator activity

No dingoes were detected on transect plots at Sturt National Park or on transects and scent stations at Mundowdna/Wilpoorina during both sampling years. Foxes and feral cats were detected at all of the study sites. Transect data showed between-site and between-year variation in activity indices for dingoes and foxes, but not for feral cats (Table 1). When mean daily visitation rates for each predator species were compared, the proportion of scent stations visited was similar across sampling nights, indicating minimal variation in animal activity. Residual deviance for all predator species was < 1, indicating no evidence of overdispersion after taking into account the random effects of the model.

Activity of dingoes on transects varied between sites ($P < 0.001$) and sampling years ($P = 0.02$) (Table 1). Dingo activity decreased at the site sampled 3 months post rains but increased at sites sampled one year post rains. The highest mean PAI for dingoes was found at Quinyambie Station one year post rains (PAI = 0.85). The highest proportion of scent station visitations by dingoes was recorded at Quinyambie Station during both sampling periods (pr = 26.3% and 24.8%). followed by Finniss Springs (pr = 19.2% and 16.8%) and then Bollards Lagoon (pr = 9.9% and 14.9%). Mean activity indices from scent stations also showed a difference in dingo activity between sites ($P < 0.001$) and across years for all sites ($P = 0.01$), but no interaction effect was detected (Table 2).

As with dingoes, activity of foxes on transects varied between sites ($P = 0.002$) and between years ($P = 0.04$) (Table 1). Sites sampled one year post rains saw an increase in fox activity on both transects and scent stations between sampling periods; however, differences between years in fox activity on scent stations were not significant ($P = 0.10$) (Table 1). The highest activity estimates for foxes were recorded at Sturt National Park 3 months post rains (PAI = 0.74), while fox activity was lowest at Quinyambie Station 3 months post rainfall (PAI = 0.04). Similarly, fox visitation rates recorded on scent stations were highest at Sturt National Park (pr =17.8% and 34.7%) and Mundowdna/Wilpoorina (pr = 24.9% and 13.1%), while the lowest recorded visitation rates for foxes at scent stations were found at Quinyambie Station during both years of sampling (pr = 1.5% and

Downloaded from http://meridian.allenpress.com/australian-zoologist/article-pdf/41/3/417/3125756/i0067-2238-41-3-417.pdf by guest on 13 March 2024

Table 1. Probability (P) values shown for the effects of site and year on estimated passive activity index (PAI) and mean activity indices (MAI). Corresponding residuals (R) and standard error (pooled) values for predator species and prey categories are given. * denotes significant (P < 0.05) and ** highly significant (P < 0.005) result; n.d. indicates statistic not available.

Species/Category	Site	Year	Site × Year	R	+ s.e
PAI (transects)					
Dingo	< 0.001**	0.016*	0.778	0.113	0.026
Fox	0.002**	0.158	0.036*	0.077	0.017
Feral cat	0.488	0.496	0.993	0.013	0.003
Macropod	0.005*	0.032	0.046*	0.044	0.009
Rabbit	< 0.001**	0.127	0.133	5.142	1.163
Reptile	0.051	0.197	0.891	32.89	8.22
Small mammal (all sites)	< 0.001**	< 0.002**	< 0.004**	9.196	2.299
Small mammal (excluding Quinyambie station)	< 0.001**	0.212	n.d.	0.324	0.094
MAI (scent stations)					
Dingo	< 0.001**	0.011*	0.787	0.009	0.002
Fox	0.033*	0.097	0.158	0.018	0.004
Feral cat	0.320	0.856	0.332	0.002	0.001

Table 2. The modelled proportion of scent stations (*pr*) visited by dingoes, foxes and feral cats at each study site by sampling year, including 95% confidence intervals (C.I.).

Site	Rainfall	Dingos pr % (95% C.I.)	Foxes pr % (95% C.I.)	Feral Cats pr % (95% C.I.)
Sturt National Park	Prior to rains	0.0	17.8 (6.1 - 42.1)	1.3 (0.1 - 11.0)
	Post rainfall (3 months)	0.8 (0.1 - 4.5)	34.7 (15.1 - 61.5)	1.5 (0.3 - 8.4)
Bollards Lagoon	Prior to rains	9.9 (3.7 - 23.9)	0.0	5 (0.8 - 26.3)
	Post rainfall (1 year)	14.9 (7.6 - 27.2)	4.7 (1.2-17.1)	3.3 (0.7 - 14.1)
Quinyambie Station	Post rainfall (3 months)	26.3 (15.7 - 40.5)	1.5 (0.2 - 8.0)	0.8 (0.1 - 6.8)
	Post rainfall (1 year)	24.8 (14.7 - 38.7)	4.5 (1.2 - 15.2)	4.8 (1.3 - 16.7)
Mundowdna	Prior to rains	0.0	24.9 (9.8 - 50.2)	1.5 (0.3-8.4)
Wilpoorina	Post rainfall (3 months)	0.0	13.1 (4.5 - 32.3)	8.2 (2.5 - 24.2)
Finnis Springs	Prior to rains	19.2 (10.2 - 33.3)	17.8 (6.2 - 41.6)	4.9 (1.1 - 18.4)
	Post rainfall (3 months)	16.8 (9.2 - 28.8)	7.9 (2.4 - 22.8)	6.1 (1.7 - 19.8)

4.5%) (Table 2). Mean activity indices calculated from fox visitations to scent stations at sites sampled 3 months post rainfall showed an increase in fox activity between sampling years at Sturt National Park, but a decrease in fox activity at Mundowdna/Wilpoorina and Finniss Springs (Table 2).

Feral cat activity on transects was fairly uniform across all sites (P = 0.49) and sampling years (P = 0.50) (Table 1). The highest PAI for feral cats was recorded at Finniss Springs prior to rains (PAI = 0.18), while the lowest feral cat activity was recorded at Sturt National Park three months post rainfall (PAI = 0.04). Mean activity indices

Downloaded from http://meridian.allenpress.com/australian-zoologist/article-pdf/41/3/417/3125756/i0067-2238-41-3-417.pdf by guest on 13 March 2024

for feral cats calculated from scent station visitations did not differ across sites (P = 0.32) or years (P = 0.86) (Table 1). Feral cats were detected on scent stations at all study sites during both sampling years, but visitation rates were low and showed no clear pattern. Visitation rates for feral cats were consistently low at Sturt National Park (pr = 1.3% and 1.5% respectively) but varied between sampling years within the other four study sites (Table 2). The highest visitation rates for feral cats was detected at Mundowdna/Wilpoorina 3 months post rains (pr = 8.2%), but low visitation rates were recorded prior to rains at the same site (pr = 1.5%). Similarly, a very low visitation rate for feral cats was recorded 3 months post rains at Quinyambie Springs (pr = 0.8%), but this increased to 4.8% one year post rains (Table 2).

Prey activity

Activity on transects of all prey, including macropods (P = 0.01), rabbits (P < 0.001), small mammals (P < 0.001) and reptiles (P = 0.05) differed between the study sites, although not as markedly for reptiles as other prey (Table 1. Probability (P) values shown for the effects of site and year on estimated passive activity index (PAI) and mean activity indices (MAI). Corresponding residuals (R) and standard error (pooled) values for predator species and prey categories are given. * denotes significant (P < 0.05) and ** highly significant (P < 0.005) result; n.d. indicates statistic not available.Table 1). Small mammal activity varied significantly between sites even when Quinyambie Station was removed from the analysis (P < 0.001) Table 1. Probability (P) values shown for the effects of site and year on estimated passive activity index (PAI) and mean activity indices (MAI). Corresponding residuals (R) and standard error (pooled) values for predator species and prey categories are given. * denotes significant (P < 0.05) and ** highly significant (P < 0.005) result; n.d. indicates statistic not available.(Table 1).

The first sampling period for this study took place after 5–7 years of lower-than-average annual rainfall across the region, and both predator and prey activity were the lowest recorded for most categories. Prior to rains, the activity on transects of small to medium sized prey was lower at Sturt National Park than at other sites. The highest activity estimates for small mammals (PAI = 52.71) and rabbits (PAI = 18.90) were found at Quinyambie Station one year post rains. In contrast, the highest activity estimate for macropods recorded on transects was at Sturt National Park prior to rains (PAI = 0.88). The lowest macropod activity estimates were found at Quinyambie Station during both sampling years. There was some significant variation of activity estimates between sampling years for macropods at all sites (P = 0.03) and small mammals at Quinyambie station (P < 0.002), but not for rabbits or reptilesTable 1. Probability (P) values shown for the effects of site and year on estimated passive activity index (PAI) and mean activity indices (MAI). Corresponding residuals (R) and standard error (pooled) values for predator species and prey categories are given. * denotes significant (P < 0.05) and ** highly significant (P < 0.005) result; n.d. indicates statistic not available. (Table 1).

Spotlighting results for macropods showed trends similar to transect data for all sites and years with the exception of Sturt National Park during the second year of sampling, where spotlighting found an increase in macropod activity. Activity of macropods determined by spotlighting was lowest at Finniss Springs (0 km^{-1}) and Quinyambie Station prior to rains (0.05 km^{-1}) and highest at Sturt National Park both prior to and 3 months post rains (1.267 km^{-1}; 1.358 km^{-1}, respectively). Spotlighting results for rabbits also showed similar trends to transect data for all sites and years. Activity for rabbits detected by spotlighting was lowest at Mundowdna/Wilpoorina prior to rains (0.343 km^{-1}) and was also low both prior to rain and 3 months post rainfall at Sturt National Park (0.475 km^{-1} ; 0.458 km^{-1}). Rabbit activity was highest at Quinyambie Station, being high at 3 months post rains (2.503 km^{-1}) and increased substantially one year post rains (7. 85 km^{-1}).

Discussion

The effect of dingo management and site attributes on the activity of predators and prey

An improved understanding of how ecosystems function is important for effective natural resource management and biodiversity conservation. While arid zone ecosystems are typically considered to be "bottom up", driven by primary productivity (Jaksic *et al.* 1997; Morton *et al.* 2011), this study found that dingo management was an important predictor of dingo, fox and some prey activity under varying levels of productivity. Evidence from this research showed that while the strength of trophic regulation by dingoes may fluctuate, top down effects occurred both prior to and post significant rainfall events at the study sites. In particular, strong relationships were found between dingo management, dingo activity and fox activity, and these relationships persisted regardless of rainfall. This research builds on the findings of other Australian arid zone studies that have examined the relative importance of dingoes in the suppression of mesopredators, including top down effects on prey, during periods of different productivity (Letnic *et al.* 2011; Greenville *et al.* 2014).

In this study, and consistent with the theory of top down regulation, dingoes appeared to suppress fox activity where dingoes were uncontrolled or only opportunistically controlled. At sites where dingoes were absent or in low numbers, fox activity was higher, with the highest fox activity at sites where dingoes were controlled through exclusion fencing. Similar to the findings of Newsome *et al.* (2001), fox activity was up to 22 times higher in the absence of dingoes. An inverse relationship between

Downloaded from http://meridian.allenpress.com/australian-zoologist/article-pdf/41/3/417/3125756/i0067-2238-41-3-417.pdf by guest on 13 March 2024

the abundance of dingoes and foxes has been reported in many arid zone studies (Short and Smith 1994; Johnson *et al.* 2007; Letnic *et al.* 2009a, b; Letnic and Koch 2010). Both fox and dingo activity were lower at sites where 1080 poison baiting was conducted (McIlroy *et al.* 1986; McIlroy 1992; Allen 2000; Thomson *et al.* 2000; Allen and Sparkes 2001).

Similar to the findings of Fancourt *et al.* (2019), this study found that while dingo management appeared to have a strong effect on dingo and fox activity, it did not appear to be an important determinant of feral cat activity. Activity estimates for feral cats at all sites were low, as is typical in arid environments (Edwards *et al.* 2000; Read and Bowen 2001), and were fairly uniform between sites and years (Newsome *et al.* 2001; Letnic *et al.* 2009b). Feral cat activity was not strongly correlated with either dingo or fox activity, although feral cats appeared less active overall in the presence of high fox activity. This is consistent with other studies that found feral cats to increase in density when foxes were controlled (Christensen and Burrows 1994; Molsher 1998; Risbey *et al.* 1999; Risbey *et al.* 2000; Read and Bowen 2001; Holden and Mutze 2002).

Dingoes, foxes and feral cats are all opportunistic, generalist predators and as such have an impact on a wide variety of prey (Dickman 1996; Doherty *et al.* 2019). Macropods have been found to be the most common prey item for dingoes in many studies (Whitehouse 1977; Shepherd 1981; Newsome *et al.* 1983a, b; Thomson 1992a) and are of particular importance when rabbits occur in low densities or decline during drought (Newsome *et al.* 1983a; Thomson 1992a). An inverse relationship was found between dingo and macropod activity, with macropod activity highest in the absence of dingoes, even when surface water was limited (Sturt National Park) or where macropods were regularly harvested, and productivity was low (Mundowdna/Wilpoorina). Previous research has found that dingoes can limit macropod populations (Corbett and Newsome 1987; Caughley *et al.* 1980; Marsack and Campbell 1990; Pople *et al.* 2000).

Predation is also an important limiting factor for rabbit populations (Pech *et al.* 1992, 1995; Risbey *et al.* 2000). Where rabbits are abundant in arid regions, all three predators target them as primary prey (Bayley 1978; Corbett and Newsome 1987; Catling 1988; Molsher *et al.* 1999; Risbey *et al.* 1999). Rabbits are found on both sides of the DBF; however, larger increases in rabbit populations occur in areas where dingo populations remain (Newsome *et al.* 2001). This pattern in rabbit abundance has been previously attributed to a lack of competition from sheep grazing (Newsome *et al.* 2001) but may also be associated with a reduction in fox predation. In this study, a strong inverse relationship between fox and rabbit activity was found, and there was a trend for feral cat activity to mirror rabbit activity. Previous studies have shown increases in fox and feral cat densities following increased rabbit abundance (Morton 1990; Molsher *et al.* 1999; Holden and Mutze 2002; Read *et al.* 2008) and that the combined predation of foxes and feral cats can regulate rabbit populations at low densities (Pech *et al.* 1992, 1995; Banks 2000). When foxes are controlled, rabbits have been shown to increase 6–12 times their initial abundance (Newsome *et al.* 1989; Banks *et al.* 1998).

Rabbits increase their sensitivity to predation impacts when activity is very low (Pech *et al.* 1992; Salo *et al.* 2010). With the exception of Quinyambie Station, rabbit activity was low at all study sites, but was lowest at Sturt National Park, where fox activity was uniformly high. In the absence of dingoes, foxes maintained high activity levels during times of low rabbit activity, likely through utilizing alternative food resources, such as carcasses (Holden and Mutze 2002; Paltridge 2002). Supplementary food resources can sustain artificially high predator populations during times of low prey availability (Corbett and Newsome 1987; Pech *et al.* 1995; Pech and Hood 1998; Courchamp *et al.* 1999), leading to suppressive effects on prey populations to an extent that prey become trapped in a "predator pit" (Newsome 1990) and unable to increase, even in response to rains (Smith and Quin 1996). At Sturt National Park, it is likely that the drought-induced availability of macropod carcasses as an alternative food resource has led to artificially high densities of foxes prior to rains and consistent low activity of rabbits, even post rainfall (Pech *et al.* 1992; Krebs 1996; Banks *et al.* 2000).

One further consideration that influences rabbit activity is the spread of Rabbit Haemorrhagic Disease (RHD) after rains. RHD was reported at Bollards Lagoon during summer 2007 (G. Rieck, pers. comm., April 2008) and affected rabbit populations at Mundowdna/Wilpoorina in September 2006 (P. Litchfield, pers. comm., January 2007). No RHD was reported at Quinyambie Station during sampling, and high activity estimates for rabbits were recorded in comparison to other high productivity sites. When rabbits are at high densities, previous research suggests that environmental fluctuations are more important than predation in regulating abundance (Cooke 1982; Newsome *et al.* 1989).

The combined pressures of predation and RHD may lead to reduced rabbit numbers and an increase in predation on alternative prey, such as small mammals and reptiles (Pech and Hood 1998; Courchamp *et al.* 1999; Blumstein *et al.* 2004). The lowest activity estimates for small mammal and reptiles both were prior to and post rains at Sturt National Park under high fox densities. On the neighbouring property of Bollards Lagoon, where baiting of both canid species occurred, higher levels of small vertebrate activity were recorded.

In contrast to fox activity, there appeared to be no clear pattern that would suggest a significant relationship between feral cat activity and the activity of small vertebrates. Even though small vertebrates are an

Downloaded from http://meridian.allenpress.com/australian-zoologist/article-pdf/41/3/417/3125756/i0067-2238-41-3-417.pdf by guest on 13 March 2024

important dietary item for feral cats (Bayley 1978; Catling 1988; Risbey *et al.* 1999; Eldridge *et al.* 2002), evidence for negative impacts of feral cats on small vertebrate populations remains inconsistent (Risbey *et al.* 2000; Eldridge *et al.* 2002). With the exception of Sturt National Park, reptile activity was similar among sites, but small mammals were estimated to have the highest activity indices where dingoes were present and productivity was high, and the lowest activity where fox activity was highest and productivity lowest. Hunter *et al.* (2018) found that dingo removal had a negative effect on the abundance of native mammals weighing less than the critical weight range of 35-5500 g. Small mammal activity was also low at low productivity sites even in the presence of dingoes, and thus appeared to be influenced by a combination of predator activity and site productivity (Dickman 1996; Dickman *et al.* 1999, 2001). We observed that the activity of small vertebrates, particularly mammals, was distributed patchily across sites and there was large disparity between sampling areas. Possible reasons for this inconsistency may be variation in microhabitats, grazing patterns or patchiness of rainfall (Westbrooke *et al.* 2005; Yarnell *et al.* 2007).

Activity of predators and prey after a significant rainfall event

In arid environments, the impact of rainfall on animal activity occurs primarily in three ways. First, mobile species may disperse as surface water becomes available in previously water remote areas (Ealey 1967; Corbett 1995). A large rainfall event would lead to surface water becoming more readily available, enabling mobile prey species to disperse rapidly to areas of new growth, with predators following prey movements (Sinclair 1983).

Prior to rains at sites with few permanent waters, such as Finniss Springs and Sturt National Park, both predators and prey would have been spatially restricted, placing intense pressure on food resources surrounding remaining surface water. At Sturt National Park, fox presence on transects increased immediately following rains, suggesting an increase in dispersive movements. At the same site, a large increase in macropod activity detected by spotlighting revealed that macropods had also dispersed to areas away from permanent waters to access new vegetative growth. Similarly, a decrease in canid activity on transects following rains at Finniss Springs may have been due to the movement away from sampling sites as creeks and drainage lines provided an abundance of surface water across the site. Dispersal after rains may not be as evident at pastoral sites, where artificial water resources for stock are distributed evenly across the landscape, enabling predators and prey to be more homogeneously distributed on a continual basis (James *et al.* 1999).

Second, increases in primary productivity lead to increases in prey activity and abundance. The "bottom up" response of desert-dwelling vertebrates to large rainfall events includes immediate increases in activity and dispersal to productive "hot-spots" (Grant and Scholes 2006; Abere and Oguzor 2011) as well as reproductive stimulation in response to sudden increases in primary productivity (James 1991; Masters 1993; Soliman and Mohallal 2009; Medger *et al.* 2010). Predators may initially respond to such increases in prey with changes in activity, while increased predator densities as a result of high juvenile recruitment and survivorship occur the following breeding season (Pech *et al.* 1995; Previtali *et al.* 2009). Rainfall is known to initiate breeding in both rabbits (Wood 1980) and small mammals (Dickman *et al.* 1999); indeed, a massive eruption of two species of native hopping mice (*Notomys fuscus* and *N. alexis*) was found at Quinyambie Station immediately post rainfall. One year after the rainfall event, activity of small mammals at this site continued to increase significantly, while increases in small prey at less productive sites or where dingoes were absent were more marginal. In addition to direct predation by mesopredators, small prey may also change their activity based on perceived predation risk. Where dingoes are retained in an ecosystem and mesopredator activity is lower, this perceived risk may be reduced, increasing small prey activity (Gordon *et al.* 2015).

Third, due to the prey switching tactics of opportunistic, generalist predators, time since rainfall alters predation impacts on different prey species (Corbett and Newsome 1987; Randa *et al.* 2009; Tatler *et al.* 2019). Mammalian carnivores display great flexibility in hunting behaviours, and the practice of prey switching in many species allows for exploitation of alternate food resources around fluctuating staple prey (Curio 1976; Randa *et al.* 2009). Previous studies in Australia suggest that when preferred prey is scarce, such as during drought, reptiles and carrion play an important role in sustaining predator populations (Whitehouse 1977; Bayley 1978; Paltridge 2002). Immediately after rains, small mammals increase and, due to both their availability and 'catchability', are targeted by all three predator species (Corbett and Newsome 1987; Eldridge *et al.* 2002; Tatler *et al.* 2019).

In this study, when the activity of a preferred prey (rabbits) was low, activity of small vertebrates was significantly lower where dingoes were absent and fox activity was high. The flexible social structure of dingoes allows them to exploit larger prey such as adult macropods and livestock when rabbits decline (Newsome *et al.* 1983a; Thomson 1992a; Tatler *et al.* 2019). In contrast, mesopredators switch to targeting smaller prey such as small mammals or reptiles (Molsher *et al.* 1999; Read and Bowen 2001). Foxes do prey on juvenile macropods (Banks *et al.* 2000); however, their impact would likely be limited to lowering recruitment during flush periods as they prey only on one life stage of the population (Russell *et al.* 2009). While dingoes

Downloaded from http://meridian.allenpress.com/australian-zoologist/article-pdf/41/3/417/3125756/i0067-2238-41-3-417.pdf by guest on 13 March 2024

may periodically target small mammals (Corbett and Newsome 1975; Tatler *et al.* 2019), mesopredators would likely have a more consistent and larger cumulative impact overall on these prey in the long term (Banks *et al.* 2004). These findings support the premise that where dingoes are retained in the ecosystem, there may exist more stable populations of smaller prey that allow a larger and more rapid response to rainfall (Pech *et al.* 1992; Short and Smith 1994; Banks 2000; Letnic and Koch 2010; Tatler *et al.* 2019).

It is important to consider these results in light of the limitations of this study. First, it is difficult to assess the effect that unmeasured native predators, such as raptors and reptiles, may have on prey populations. For example, large varanids are able to increase in abundance where other predators are controlled and would likely have a significant impact on prey populations under such circumstances (Lloyd 2007; Sutherland *et al.* 2011). Second, not all prey species were measured. Invertebrates can form a major part of mesopredator diets during drought, and birds have been found in both fox and cat diets in arid regions (Catling 1988; Read and Bowen 2001). However, the long term key interactions in arid Australia appear to occur between predators and their primary prey of macropods, rabbits and small mammals (Corbett and Newsome 1987; Newsome *et al.* 1989; Newsome 1990; Pech *et al.* 1992, 1995; Pech and Hood 1998; Newsome *et al.* 2001; Davey *et al.* 2006) on which this study focused.

Rainfall and regulation: A Baseline Density Theory

The outcomes of this study suggest that the top down effects of an apex predator, the dingo, may play a role in mesopredator limitation and trophic regulation in arid ecosystems. In this study, predator activity fluctuated in response to rainfall; at most sites where dingoes, foxes and feral cats co-existed, all three species increased their activity with increasing prey. However, in the presence of dingoes, fox activity did not increase to levels found at sites where dingoes were absent. While the strength of intraguild interactions may vary with dingo density, site productivity and amount of rainfall, results from this study suggest that dingo-fox interactions are present even when productivity and prey availability is high. These findings are supported by previous research on dingo, mesopredator, and prey interactions in arid ecosystems during periods of different productivity (Letnic *et al.* 2011; Greenville *et al.* 2014).

The mechanism behind the influence of dingoes on ecosystem trophic dynamics is likely two-fold. First, consistent with the theory of top down regulation (Soulé *et al.* 1988), dingoes may both limit and regulate fox populations. Sinclair (1989) defined population regulation as the process by which a population returns

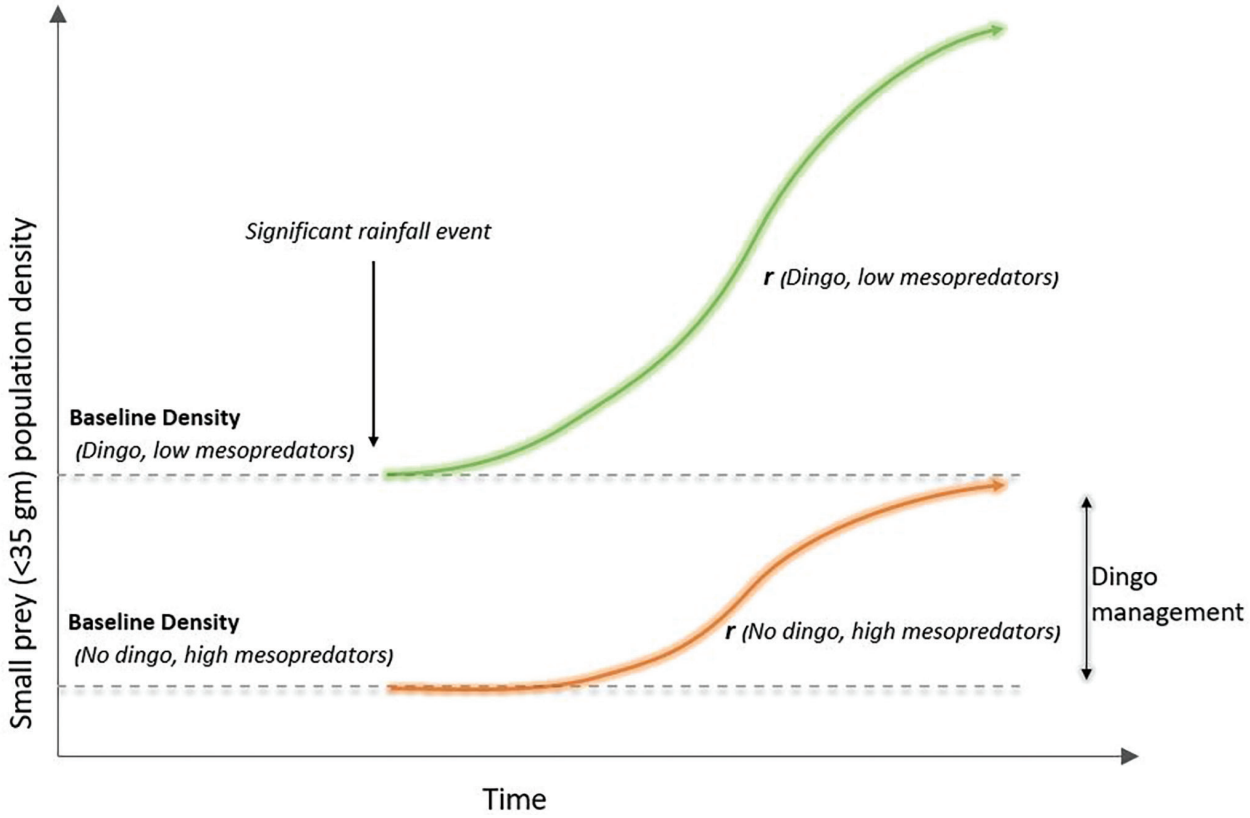

Figure 2. Theoretical rate of increase of small prey density after a rainfall event at a given site under differing dingo management regimes.

Downloaded from http://meridian.allenpress.com/australian-zoologist/article-pdf/41/3/417/3125756/i0067-2238-41-3-417.pdf by guest on 13 March 2024

Figure 3. Dingo at Quinyambie Station. Photograph R. Brawata, 2006.

to its equilibrium density, and population limitation as the process that sets the equilibrium density. During dry times, dingoes may limit fox populations through either direct (Moseby *et al.* 2012) or indirect (Mitchell and Banks 2005; Brawata and Neeman 2011) effects, effectively decreasing the 'baseline' population from which foxes can respond to increases in prey. Dingoes may then regulate fox populations back to this equilibrium when prey decreases during 'bust' periods, maintaining lower fox activity over the long term (Sinclair *et al.* 1998).

Second, dingoes may both directly and indirectly decrease predation pressure on smaller prey, due to their ability to both limit fox populations and to utilize a wider range of prey resources. Under a management regime that retains dingoes in an arid ecosystem, top down limitation and regulation of fox populations may enable higher relative "baseline densities" of small vertebrates to persist, from which a larger and more rapid rate of increase during the "boom" periods can occur (Figure 2). Where dingoes are absent or occur at very low densities, and fox activity is high, small vertebrates would have lower relative "baseline densities" at a given site (Figure 2).

The "baseline density" refers to a density at which mesopredators or prey are maintained on average across a number of years by top down regulation, from which populations may fluctuate up and down in response to increases or decreases in resources through bottom up forces. While dingo management will likely influence the relative level of these "baseline densities" for both foxes and small vertebrate prey, the actual density is likely determined by a complex combination of environmental variables, site management, interspecific interactions and species-specific traits, such as those exhibited by cyclic and non-cyclic species (Salo *et al.* 2010).

In arid ecosystems, intraspecific competition plays an important role in the dynamics of small mammal populations (Previtali *et al.* 2009) and variation in activity and dispersal occurs between periods within boom-bust cycles (Dickman *et al.* 2010). Livestock grazing may also impact on some small mammal species (Kerley 1992) although previous studies in the Australian arid zone have found predation to be a greater determinant of small vertebrate activity (Read and Cunningham 2010). The existence of livestock also provides a supplementary food source and enables higher dingo densities to be sustained during drought (Corbett and Newsome 1987). In this study, at a site with no stock, low productivity and limited surface water availability, dingoes did not appear to suppress fox activity effectively. In addition, it is recognised that other predators such as raptors and larger reptiles, whose activity was not measured, occur within the study ecosystems and may have significant impacts on prey populations (Lloyd 2007; Sutherland *et al.* 2011). Further testing of this "Baseline Density Theory" should investigate the interaction strength between dingo management and site productivity to inform dingo management for the long-term sustainability of prey populations in the context of climate change.

Downloaded from http://meridian.allenpress.com/australian-zoologist/article-pdf/41/3/417/3125756/i0067-2238-41-3-417.pdf by guest on 13 March 2024

In conclusion, it may be that dingoes provide a net benefit to small vertebrates in arid ecosystems through reducing predatory impacts of foxes (Figure 3). Retaining dingo populations in some ecosystems may assist in the management of biodiversity over the long term, including the conservation of native fauna populations susceptible to fox predation. Improving our understanding of such trophic interactions, will assist managers in making more ecologically informed decisions about control of top order carnivores in arid areas.

Acknowledgments

This research was funded by an ARC Linkage grant LP 0455163 in collaboration with the Wilderness Society.

References

Abere, S. A. and Oguzor, N. S. 2011. Adaptation of animals to arid ecological conditions. *World Journal of Zoology* **6**(2): 209-214.

Allen, L. 2000. Measuring predator control effectiveness: reducing numbers may not reduce predator impact. *Proceedings of the Nineteenth Vertebrate Pest Conference*: 284-289. https://doi.org/10.5070/V419110174

Allen, L., Engeman, R. and Krupa, H. 1996. Evaluation of three relative abundance indices for assessing dingo populations. *Wildlife Research* **23**(2): 197-206.

Allen, L. R. and Sparkes, E. C. 2001. The effect of dingo control on sheep and beef cattle in Queensland. *Journal of Applied Ecology* **38**(1): 76-87. https://doi.org/10.1046/j.1365-2664.2001.00569.x

Altmann, J. 1996. Observational study of behaviour: sampling methods. Pp. 843 in *Foundations of Animal Behaviour: classic papers with commentaries*, edited by Lynne D. Houck and Lee C. Drickamer. University of Chicago Press in association with Animal Behavior Society, Chicago, USA.

Arnold, G. W., Steven, D. E. and Weeldenburg, J. R. 1994. Comparative ecology of western grey kangaroos (*Macropus fuliginosus*) and euros (*M. robustus erubescens*) in Durokoppin Nature-Reserve, isolated in the central wheat-belt of Western Australia. *Wildlife Research* **21**(3): 307-322.

Ballinger, A. and Morgan, D. G. 2002. Validating two methods for monitoring population size of the European rabbit (*Oryctolagus cuniculus*). *Wildlife Research* **29**(5): 431-437. https://doi.org/10.1071/WR01055

Banks, P. B. 2000. Can foxes regulate rabbit populations? *Journal of Wildlife Management* **64**(2): 401-406. DOI: 10.2307/3803238

Banks, P. B., Dickman, C. R. and Newsome, A. E. 1998. Ecological costs of feral predator control: Foxes and rabbits. *Journal of Wildlife Management* **62**(2): 766-772. DOI: 10.2307/3802353

Banks, P. B., Newsome, A. E. and Dickman, C. R. 2000. Predation by red foxes limits recruitment in populations of eastern grey kangaroos. *Austral Ecology* **25**(3): 283-291. https://doi.org/10.1046/j.1442-9993.2000.01039.x

Banks, P. B., Norrdahl, K., Nordstrom, M. and Korpimaki, E. 2004. Dynamic impacts of feral mink predation on vole metapopulations in the outer archipelago of the Baltic Sea. *Oikos* **105**(1): 79-88. https://doi.org/10.1111/j.0030-1299.2004.12855.x

Bayley, C. P. 1978. A comparison of the diets of the red fox and feral cat in an arid environment. *South Australian Naturalist* **53**: 20-28.

Bayliss, P. 1985. The population dynamics of red and western grey kangaroos in arid New South Wales, Australia.1. Population trends and rainfall. *Journal of Animal Ecology* **54**(1): 111-125. DOI: 10.2307/4624

Berry, S., Mackey, B. and Brown, T. 2007. Potential applications of remotely sensed vegetation greenness to habitat analysis and the conservation of dispersive species. *Pacific Conservation Biology* **13**: 120-127. https://doi.org/10.1071/PC070120

Blumstein, D. T., Daniel, J. C. and Springett, B. P. 2004. A test of the multi-predator hypothesis: rapid loss of antipredator behavior after 130 years of isolation. *Ethology* **110**(11): 919-934. https://doi.org/10.1111/j.1439-0310.2004.01033.x

Brawata, R. L. and Neeman, T. 2011. Is water the key? Dingo management, intraguild interactions and predator distribution around waterpoints in arid Australia. *Wildlife Research* **38**: 426-436. DOI: 10.1071/WR10169

Bruno, J. F. and Cardinale, B. J. 2008. Cascading effects of predator richness. *Frontiers in Ecology and the Environment* **6**(10): 539-546. https://doi.org/10.1890/070136

Burbidge, A. A. and McKenzie, N. L. 1989. Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. *Biological Conservation* **50**: 143-198. https://doi.org/10.1016/0006-3207(89)90009-8

Burbidge, A. A. and Manly, B. F. J. 2002. Mammal extinctions on Australian islands: causes and conservation implications. *Journal of Biogeography* **29**(4): 465-473. https://doi.org/10.1046/j.1365-2699.2002.00699.x

Catling, P. C. 1988. Similarities and contrasts in the diets of foxes, *Vulpes vulpes* and cats, *Felis catus*, relative to fluctuating prey populations and drought. *Australian Wildlife Research* **15**: 307-317. https://doi.org/10.1071/WR9880307

Downloaded from http://meridian.allenpress.com/australian-zoologist/article-pdf/41/3/417/3125756/i0067-2238-41-3-417.pdf by guest on 13 March 2024

Caughley, G., Grigg, G. C., Caughley, J. and Hill, G. J. E. 1980. Does dingo predation control the densities of kangaroos and emus? *Australian Wildlife Research* **7**(1): 1-12. https://doi.org/10.1071/WR9800001

Christensen, P. and Burrows, N. 1994. Project Desert Dreaming: experimental reintroduction of mammals to the Gibson Desert. Pp. 199-207 in *Reintroduction biology of Australian and New Zealand Fauna*, edited by M. Serena. Surrey Beatty and Sons, Chipping Norton, NSW.

Cooke, B. 1982. A shortage of water in natural pastures as a factor limiting a population of rabbits, *Oryctolagus cuniculus*, in arid, north-eastern South Australia. *Australian Wildlife Research* **9**: 465-476. https://doi.org/10.1071/WR9820465

Corbett, L. and Newsome, A. 1975. Dingo society and its maintenance: a preliminary analysis. Pp. 369-379 in *The Wild Canids*, edited by M. W. Fox. Van Nostrand Reinhold, New York, USA.

Corbett, L. K. 1995. *The Dingo in Australia and Asia*. University of New South Wales Press, Sydney.

Corbett, L. K. and Newsome, A. E. 1987. The feeding ecology of the dingo. 3. Dietary relationships with widely fluctuating prey populations in arid Australia; a hypothesis of alternation of predation. *Oecologia* **74**(2): 215-227. DOI: 10.1007/BF00379362

Courchamp, F., Langlais, M. and Sugihara, G. 1999. Cats protecting birds: modelling the mesopredator release effect. *Journal of Animal Ecology* **68**(2): 282-292. https://doi.org/10.1046/j.1365-2656.1999.00285.x

Crooks, K. R. and Soulé, M. E. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* **400**(6744): 563-566.

Curio, E. 1976. *The Ethology of Predation*. Springer-Verlag, Berlin, Germany.

Davey, C., Sinclair, A. R. E., Pech, R. P., Arthur, A. D., Krebs, C. J., Newsome, A. E., Hik, D., Molsher, R. and Allcock, K. 2006. Do exotic vertebrates structure the biota of Australia? An experimental test in New South Wales. *Ecosystems* **9**(6): 992-1008. DOI:10.1007/s10021-004-0173-0

Dickman, C. R. 1996. Impact of exotic generalist predators on the native fauna of Australia. *Wildlife Biology* **2**: 185-195. https://doi.org/10.2981/wlb.1996.018

Dickman, C. R., Haythornthwaite, A. S., McNaught, G. H., Mahon, P. S., Tamayo, B. and Letnic, M. 2001. Population dynamics of three species of dasyurid marsupials in arid central Australia: a 10-year study. *Wildlife Research* **28**(5): 493-506. https://doi.org/10.1071/WR00023

Dickman, C. R., Mahon, P. S., Masters, P. and Gibson, D. F. 1999. Long-term dynamics of rodent populations in arid Australia: the influence of rainfall. *Wildlife Research* **26**(4): 389-403. https://doi.org/10.1071/WR97057

Doherty, T. S., Davis, N. E. Dickman, C. R, Forsyth, D. M., Letnic, M. Nimmo, D. G., Palmer, R., Ritchie, E. G., Benshemesh, J. Edwards, G., Lawrence, J., Lumsden, L., Pascoe, C., Sharp, A., Stokeld, D., Myers, C., Story, G., Story, P., Triggs, B., Venosta, M., Wysong, M. and Newsome, T. M. 2019. Continental patterns in the diet of a top predator: Australia's dingo. *Mammal Review* **49**(1): 31-44. https://doi.org/10.1111/mam.12139

Ealey, E. H. M. 1967. Ecology of the euro *Macropus robustus* (Gould) in north western Australia. II. Behaviour, movement and drinking patterns. *C.S.I.R.O. Wildlife Research* **12**: 27-51. https://doi.org/10.1071/CWR9670027

Edwards, G. P., de Preu, N. D., Shakeshaft, B. J. and Crealy, I. V. 2000. An evaluation of two methods of assessing feral cat and dingo abundance in central Australia. *Wildlife Research* **27**(2): 143-149. https://doi.org/10.1071/WR98067

Eldridge, S. R., Shakeshaft, B. J. and Nano, T. J. 2002. The impact of wild dog control on cattle, native and introduced herbivores and introduced predators in central Australia. Unpublished report to the Bureau of Rural Sciences, Canberra.

Engeman, R., Allen, L. and Zerbe, G. O. 1998. Variance estimate for the Allen activity index. *Wildlife Research* **25**: 643-648. https://doi.org/10.1071/WR97073

Engeman, R. M., Pipas, M. J., Gruver, K. S. and Allen, L. 2000. Monitoring coyote population changes with a passive activity index. *Wildlife Research* **27**(5): 553-557. https://doi.org/10.1071/WR98090

Fancourt, B. A., Cremasco, P., Wilson, C., Gentle, M. N. 2019. Do introduced apex predators suppress introduced mesopredators? A multiscale spatiotemporal study of dingoes and feral cats in Australia suggests not. *Journal of Applied Ecology* **56**(12):2584-2595. DOI: 10.1111/1365-2664.13514

Fensham, R. J., Fairfax, R. J. and Archer, S. R. 2005. Rainfall, land use and woody vegetation cover change in semi-arid Australian savanna. *Journal of Ecology* **93**(3): 596-606. https://doi.org/10.1111/j.1365-2745.2005.00998.x

Feit, B., Feit, A. and Letnic, M 2019. Apex predators decouple population dynamics between mesopredators and their prey. *Ecosystems* **22**: 1606–1617. https://doi.org/10.1007/s10021-019-00360-2

Forsyth, D. M., Robley, A. J. and Reddiex, B. 2005. Review of methods used to estimate the abundance of feral cats. Final report for the Australian Government Department of the Environment and Heritage, Department of Sustainability and Environment, Canberra.

Downloaded from http://meridian.allenpress.com/australian-zoologist/article-pdf/41/3/417/3125756/i0067-2238-41-3-417.pdf by guest on 13 March 2024

Gehrt, S. D. and Prange, S. 2007. Interference competition between coyotes and raccoons: a test of the mesopredator release hypothesis. *Behavioral Ecology* **18**(1): 204-214. https://doi.org/10.1093/beheco/arl075

Greenville, A. C., Wardle, G. M., Tamayo, T. and Dickman, C. R. 2014. Bottom-up and top-down processes interact to modify intraguild interactions in resource-pulse environments. *Oecologia* **175:** 1349-1358.

Haythornthwaite, A. S. and Dickman, C. R. 2006. Distribution, abundance, and individual strategies: a multi-scale analysis of dasyurid marsupials in arid central Australia. *Ecography* **29**(3): 285-300. DOI: 10.1111/j.2006.0906-7590.04307.x

Holden, C. and Mutze, G. 2002. Impact of rabbit haemorrhagic disease on introduced predators in the Flinders Ranges, South Australia. *Wildlife Research* **29**: 615-626. https://doi.org/10.1071/WR00101

Holmgren, M., Stapp, P., Dickman, C. R., Gracia, C., Graham, S., Gutierrez, J. R., Hice, C., Jaksic, F., Kelt, D. A., Letnic, M., Lima, M., Lopez, B. C., Meserve, P. L., Milstead, W. B., Polis, G. A., Previtali, M. A., Michael, R., Sabate, S. and Squeo, F. A. 2006. Extreme climatic events shape arid and semiarid ecosystems. *Frontiers in Ecology and the Environment* **4**(2): 87-95. DOI: 10.1890/1540-9295(2006)004[0087:ECESAA]2.0.CO;2

Hunter, D. O., Lagisz, M., Leo, V., Nakagawa, S., Letnic, M. 2018. Not all predators are equal: a continent-scale analysis of the effects of predator control on Australian mammals. *Mammal Review* **48**(2):108-122. https://doi.org/10.1111/mam.12115

Gordon, C.E., Feit, A., Grüber, J. and Letnic, M. 2015. Mesopredator suppression by an apex predator alleviates the risk of predation perceived by small prey. *Proceedings of the Royal Society B-Biological Sciences* **282**(1082): https://doi.org/10.1098/rspb.2014.2870

Grant, C. C. and Scholes, M. C. 2006. The importance of nutrient hot spots in the conservation and management of large wild mammalian herbivores in semi-arid savannas. *Biological Conservation* **130**(3): 426-437. https://doi.org/10.1016/j.biocon.2006.01.004

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* **54**(2): 187-211. https://doi.org/10.2307/1942661

Jaksic, F. M., Silva, S. I., Meserve, P. L. and Gutierrez, J. R. 1997. A long-term study of vertebrate predator responses to an El Nino (ENSO) disturbance in western South America. *Oikos* **78**(2): 341-354. DOI: 10.2307/3546302

James, C. D. 1991. Annual variation in reproductive cycles of scincid lizards (*Ctenotus*) in central Australia. *Copeia* **1991**(3): 744-760. DOI: 10.2307/1446402

James, C. D., Landsberg, J. and Morton, S. R. 1999. Provision of watering points in the Australian arid zone: a review of effects on biota. *Journal of Arid Environments* **41**(1): 87-121. https://doi.org/10.1006/jare.1998.0467

Johnson, C. N., Isaac, J. L. and Fisher, D. O. 2007. Rarity of a top predator triggers continent-wide collapse of mammal prey: dingoes and marsupials in Australia. *Proceedings of the Royal Society B-Biological Sciences* **274**(1608): 341-346. https://doi.org/10.1098/rspb.2006.3711

Johnson, C. N. and VanDerWal, J. 2009. Evidence that dingoes limit abundance of a mesopredator in eastern Australian forests. *Journal of Applied Ecology* **46**(3): 641-646. https://doi.org/10.1111/j.1365-2664.2009.01650.x

Kennedy, M., Phillips, B. L., Legge, S., Murphy, S. A. and Faulkner, R. A. 2011. Do dingoes suppress the activity of feral cats in northern Australia? *Austral Ecology* **37**(1): 134-139. https://doi.org/10.1111/j.1442-9993.2011.02256.x

Kerley, G. I. H. 1992. Ecological correlates of small mammal community structure in the semi-arid Karoo, South Africa. *Journal of Zoology* **227**: 17-27. https://doi.org/10.1111/j.1469-7998.1992.tb04341.x

Krebs, C. J. 1996. Population cycles revisited. *Journal of Mammalogy* **77**(1): 8-24. https://doi.org/10.2307/1382705

Letnic, M., Crowther, M. S. and Koch, F. 2009a. Does a top predator provide an endangered rodent with refuge from an invasive mesopredator? *Animal Conservation* **12**(4): 302-312. https://doi.org/10.1111/j.1469-1795.2009.00250.x

Letnic, M. and Dickman, C. R., 2006. Boom means bust: Interactions between the El Nino/Southern Oscillation (ENSO), rainfall and the processes threatening mammal species in arid Australia. *Biodiversity and Conservation* **15**(12): 3847-3880.

Letnic, M., Greenville, A., Denny, E., Dickman, C. R., Tischler, M., Gordon, C. and Koch, F. 2010. Does a top predator suppress the abundance of an invasive mesopredator at a continental scale? *Global Ecology and Biogeography* **20**(2): 343-353. DOI: 10.1111/j.1466-8238.2010.00600.x

Letnic, M. and Koch, F. 2010. Are dingoes a trophic regulator in arid Australia? A comparison of mammal communities on either side of the dingo fence. *Austral Ecology* **35**(2): 167-175. https://doi.org/10.1111/j.1442-9993.2009.02022.x

Letnic, M., Koch, F., Gordon, C., Crowther, M. S. and Dickman, C. R. 2009b. Keystone effects of an alien top-predator stem extinctions of native mammals. *Proceedings of the Royal Society B-Biological Sciences* **276**(1671): 3249-3256. https://doi.org/10.1098/rspb.2009.0574

Downloaded from http://meridian.allenpress.com/australian-zoologist/article-pdf/41/3/417/3125756/i0067-2238-41-3-417.pdf by guest on 13 March 2024

Letnic, M., Story, P., Story, G. Field, J., Brown, O. and Dickman, C. R. 2011. Resource pulses, switching trophic control, and the dynamics of small mammal assemblages in arid Australia. *Journal of Mammalogy* **92**(6):1210-1222. https://doi.org/10.1644/10-MAMM-S-229.1

Letnic, M., Tamayo, B. and Dickman, C. R. 2005. The responses of mammals to La Nina (El Nino Southern Oscillation)-associated rainfall, predation, and wildfire in central Australia. *Journal of Mammalogy* **86**(4): 689-703. https://doi.org/10.1644/1545-1542(2005)086[0689:TROMTL]2.0.CO;2

Lloyd, P. 2007. Predator control, mesopredator release, and impacts on bird nesting success: a field test. *African Zoology* **42**(2): 180-186. https://doi.org/10.3377/1562-7020(2007)42[180:PCMRAI]2.0.CO;2

Mahon, P. S., Banks, P. B. and Dickman, C. R. 1998. Population indices for wild carnivores: a critical study in sand-dune habitat, south-western Queensland. *Wildlife Research* **25**(1): 11-22. https://doi.org/10.1071/WR97007

Marlow, N. J. 1992. 'The ecology of the introduced red fox (*Vulpes vulpes*) in the arid zone'. PhD Thesis, University of New South Wales.

Marsack, P. and Campbell, G. 1990. Feeding behaviour and diet of dingoes in the Nullarbor Region, Western Australia. *Australian Wildlife Research* **17**(4): 349-357. https://doi.org/10.1071/WR9900349

Masters, P. 1993. The effects of fire-driven succession and rainfall on small mammals in spinifex grassland at Uluru National Park, Northern Territory. *Wildlife Research* **20**(6): 803-813. https://doi.org/10.1071/WR9930803

McIlroy, J. C. 1992. The effect on Australian animals of 1080 poisoning campaigns. *Proceedings of the 15th annual vertebrate pest conference*, University of Nebraska, Lincoln. University of California, Davis, USA.

McIlroy, J. C., Cooper, R. J., Gifford, E. J., Green, B. F. and Newgrain, K. W. 1986. The effect on wild dogs, *Canis familiaris*, of 1080 poisoning campaigns in Kosciusko National Park, NSW. *Australian Wildlife Research* **13**(4): 535-544. https://doi.org/10.1071/WR9860535

Medger, K., Chimimba, C. T. and Bennett, N. C. 2010. Seasonal reproduction in the female spiny mouse from South Africa. *Journal of Zoology* **282**(3): 163-170. https://doi.org/10.1111/j.1469-7998.2010.00726.x

Mitchell, B. D. and Banks, P. B. 2005. Do wild dogs exclude foxes? Evidence for competition from dietary and spatial overlaps. *Austral Ecology* **30**(5): 581-591. https://doi.org/10.1111/j.1442-9993.2005.01473.x

Molsher, R. 1998. Interactions between feral cats and red foxes in NSW: evidence for competition? *Proceedings of the 11th Australian Vertebrate Pest Control Conference, Perth*. VPRS, Agriculture Western Australia, Perth.

Molsher, R., Newsome, A. and Dickman, C. 1999. Feeding ecology and population dynamics of the feral cat (*Felis catus*) in relation to the availability of prey in central-eastern New South Wales. *Wildlife Research* **26**(5): 593-607. https://doi.org/10.1071/WR98058

Molsher, R. L., Gifford, E. J. and McIlroy, J. C. 2000. Temporal, spatial and individual variation in the diet of red foxes (*Vulpes vulpes*) in central New South Wales. *Wildlife Research* **27**(6): 593-601. https://doi.org/10.1071/WR99015

Morton, S. R. 1990. The impact of European settlement on the vertebrate animals of arid Australia: a conceptual model. *Proceedings of the Ecological Society of Australia* **16**: 201-213.

Morton, S. R., Stafford Smith, D. M., Dickman, C. R., Dunkerley, D. L., Friedel, M. H., McAllister, R. R. J., Reid, J. R.W., Roshier, D. A., Smith, M. A., Walsh, F. J., Wardle, G. M., Watson, I. W. and Westoby M. 2011. A fresh framework for the ecology of arid Australia. *Journal of Arid Environments* **75**: 313-329. https://doi.org/10.1016/j.jaridenv.2010.11.001

Moseby, K. E., Neilly, H., Read, J., and Crisp, H. 2012. Interactions between a top order predator and exotic mesopredators in the Australian rangelands. *International Journal of Ecology* **2012**: Article ID 250352, 15 pages. https://doi.org/10.1155/2012/250352

Mutze, G., Bird, R., Kovaliski, J., Peacick, D., Jennings, S. and Cooke, B. 2002. Emerging epidemiological patterns in rabbit haemorrhagic disease, its interaction with myxomatosis, and their effects on rabbit populations in South Australia. *Wildlife Research* **29**: 577-590. https://doi.org/10.1071/WR00100

Newsome, A. 1990. The control of vertebrate pests by vertebrate predators. *Trends in Ecology & Evolution* **5**(6): 187-191. https://doi.org/10.1016/0169-5347(90)90208-U

Newsome, A. E., Catling, P. C., Cooke, B. D. and Smyth, R. 2001. Two ecological universes separated by the Dingo Barrier Fence in semi-arid Australia: interactions between landscapes, herbivory and carnivory, with and without dingoes. *Rangeland Journal* **23**(1): 71-98. https://doi.org/10.1071/RJ01015

Newsome, A. E., Catling, P. C. and Corbett, L. K. 1983a. The feeding ecology of the dingo. 2. Dietary and numerical relationships with fluctuating prey populations in south eastern Australia. *Australian Journal of Ecology* **8**(4): 345-366. https://doi.org/10.1111/j.1442-9993.1983.tb01332.x

Downloaded from http://meridian.allenpress.com/australian-zoologist/article-pdf/41/3/417/3125756/i0067-2238-41-3-417.pdf by guest on 13 March 2024

Newsome, A. E., Corbett, L. K., Catling, P. C. and Burt, R. J. 1983b. The feeding ecology of the dingo. 1. Stomach contents from trapping in south eastern Australia, and the non-target wildlife also caught in dingo traps. *Australian Wildlife Research* **10**(3): 477-486. https://doi.org/10.1071/WR9830477

Newsome, A. E., Parer, I. and Catling, P. C. 1989. Prolonged prey suppression by carnivores: predator removal experiments. *Oecologia* **78**(4): 458-467. DOI: 10.1007/BF00378734

Paltridge, R. 2002. The diets of cats, foxes and dingoes in relation to prey availability in the Tanami Desert, Northern Territory. *Wildlife Research* **29**(4): 389-403. https://doi.org/10.1071/WR00010

Paltridge, R., Gibson, D. and Edwards, G. 1997. Diet of the feral cat (*Felis catus*) in central Australia. *Wildlife Research* **24**(1): 67-76. https://doi.org/10.1071/WR96023

Pavey, C. R., Eldridge, S. R. and Heywood, M. 2008. Population dynamics and prey selection of native and introduced predators during a rodent outbreak in arid Australia. *Journal of Mammalogy* **89**(3): 674-683. https://doi.org/10.1644/07-MAMM-A-168R.1

Pech, R. P. and Hood, G. R. 1998. Foxes, rabbits, alternative prey and rabbit calicivirus disease: consequences of a new biological control agent for an outbreaking species in Australia. *Journal of Applied Ecology* **35**(3): 434-453. https://doi.org/10.1046/j.1365-2664.1998.00318.x

Pech, R. P., Sinclair, A. R. E., Newsome, A. E. and Catling, P. C. 1992. Limits to predator regulation of rabbits in Australia: evidence from predator removal experiments. *Oecologia* **89**: 102-112. DOI: 10.1007/BF00319021

Pech, R. P., Sinclair, A. R. E. and Newsome, A. E. 1995. Predation models for primary and secondary prey species. *Wildlife Research* **22**(1): 55-64.

Pianka, E. R. 1978. *Evolutionary Ecology*. Harper and Row, New York, USA.

Poole, D. W., Cowan, D. P. and Smith, G. C. 2003. Developing a census method based on sight counts to estimate rabbit (*Oryctolagus cuniculus*) numbers. *Wildlife Research* **30**(5): 487-493. https://doi.org/10.1071/WR02014

Pople, A. R., Grigg, G. C., Cairns, S. C., Beard, L. A. and Alexander, P. 2000. Trends in the numbers of red kangaroos and emus on either side of the South Australian dingo fence: evidence for predator regulation? *Wildlife Research* **27**(3): 269-276. https://doi.org/10.1071/WR99030

Previtali, M. A., Lima, M., Meserve, P. L., Kelt, D. A. and Gutierrez, J. R. 2009. Population dynamics of two sympatric rodents in a variable environment: rainfall, resource availability, and predation. *Ecology* **90**(7): 1996-2006. DOI: 10.1890/08-0405.1

Randa, L. A., Cooper, D. M., Meserve, P. L. and Yunger, J. A. 2009. Prey switching of sympatric canids in response to variable prey abundance. *Journal of Mammalogy* **90**(3): 594-603. DOI: 10.1644/08-MAMM-A-092R1.1

Read, J. and Bowen, Z. 2001. Population dynamics, diet and aspects of the biology of feral cats and foxes in arid South Australia. *Wildlife Research* **28**(2): 195-203.

Read, J. L., Carter, J., Moseby, K. M. and Greenville, A. 2008. Ecological roles of rabbit, bettong and bilby warrens in arid Australia. *Journal of Arid Environments* **72**(11): 2124-2130. DOI: 10.1016/j.jaridenv.2008.06.018

Read, J. L. and Cunningham, R. 2010. Relative impacts of cattle grazing and feral animals on an Australian arid zone reptile and small mammal assemblage. *Austral Ecology* **35**(3): 314-324. DOI: 10.1111/j.1442-9993.2009.02040.x

Risbey, D. A., Calver, M. C. and Short, J. 1999. The impact of cats and foxes on the small vertebrate fauna of Heirisson Prong, Western Australia. I. Exploring potential impact using diet analysis. *Wildlife Research* **26**(5): 621-630. https://doi.org/10.1071/WR98066

Risbey, D. A., Calver, M. C., Short, J., Bradley, J. S. and Wright, I. W. 2000. The impact of cats and foxes on the small vertebrate fauna of Heirisson Prong, Western Australia. II. A field experiment. *Wildlife Research* **27**(3): 223-235. https://doi.org/10.1071/WR98092

Russell, J. C., Lecomte, V., Dumont, Y. and Le Corre, M. 2009. Intraguild predation and mesopredator release effect on long-lived prey. *Ecological Modelling* **220**(8): 1098-1104. DOI: 10.1016/j.ecolmodel.2009.01.017

Salo, P., Banks, P. B., Dickman, C. R. and Korpimäki, E. 2010. Predator manipulation experiments: impacts on populations of terrestrial vertebrate prey. *Ecological Monographs* **80**(4): 531-546. DOI: 10.2307/20787448

Shepherd, N. C. 1981. Predation of red kangaroos, *Macropus rufus*, by the dingo, *Canis familiaris dingo*, in north western New South Wales. *Australian Wildlife Research* **8**(2): 255-262. https://doi.org/10.1071/WR9810255

Short, J. and Smith, A. 1994. Mammal decline and recovery in Australia. *Journal of Mammalogy* **75**(2): 288-297. https://doi.org/10.2307/1382547

Sinclair, A. R. E. 1983. The function of distance movements in vertebrates. Pp. 240-258 in *The Ecology of Animal Movement*, edited by Ian R. Swingland and Paul J. Greenwood. Clarendon Press, Oxford, UK.

Sinclair, A. R. E. 1989. Population regulation in animals. Pp. 197-241 in *Ecological Concepts*, edited by J. M. Cherrett. Blackwell Scientific Publications, Oxford, UK.

Downloaded from http://meridian.allenpress.com/australian-zoologist/article-pdf/41/3/417/3125756/i0067-2238-41-3-417.pdf by guest on 13 March 2024

Sinclair, A. R. E., Pech, R. P., Dickman, C. R., Hik, D., Mahon, P. and Newsome, A. E. 1998. Predicting effects of predation on conservation of endangered prey. *Conservation Biology* **12**(3): 564-575. https://doi.org/10.1111/j.1523-1739.1998.97030.x

Smith, A. P. and Quin, D. G. 1996. Patterns and causes of extinction and decline in Australian conilurine rodents. *Biological Conservation* **77**(2-3): 243-267. DOI: 10.1016/0006-3207(96)00002-X

Soliman, S. and Mohallal, E. M. 2009. Patterns of reproduction in two sympatric gerbil species in arid Egypt. *Integrative Zoology* **4**(2): 248-253. DOI: 10.1111/j.1749-4877.2009.00157.x

Soulé, M. E., Bolger, D. T., Alberts, A. C., Wright, J., Sorice, M. and Hill, S. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology* **2:** 75–92. https://doi.org/10.1111/j.1523-1739.1988.tb00337.x

Sutherland, D. R., Glen, A. S. and de Tores, P. J. 2011. Could controlling mammalian carnivores lead to mesopredator release of carnivorous reptiles? *Proceedings of the Royal Society B-Biological Sciences* **278**(1706): 641-648. https://doi.org/10.1098/rspb.2010.2103

Tatler, J., Prowse, T. A. A., Roshier, D. A., Allen, B. L., Cassey, P. 2019. Resource pulses affect prey selection and reduce dietary diversity of dingoes in arid Australia**.** *Mammal Review* **49** (3): 263-275. https://doi.org/10.1111/mam.12157

Terborgh, J. and Estes, J. A. 2010. *Trophic Cascades: Predators, Prey and the Changing Dynamics of Nature*. Island Press, Washington, D.C., USA.

Thomson, P. C. 1992a. The behavioural ecology of dingoes in north-western Australia. III. Hunting and feeding behaviour, and diet. *Wildlife Research* **19**(5): 531-541. https://doi.org/10.1071/WR9920531

Thomson, P. C. 1992b. The behavioural ecology of dingoes in north-western Australia. IV. Social and spatial organization, and movements. *Wildlife Research* **19**(5): 543-563. https://doi.org/10.1071/WR9920543

Thomson, P. C. and Marsack, P. R. 1992. Aerial baiting of dingoes in arid pastoral areas with reference to rabies control. *Wildlife Rabies Contingency Planning in Australia* **11**: 125-134.

Thomson, P. C., Marlow, N. J., Rose, K. and Kok, N. E. 2000. The effectiveness of a large-scale baiting campaign and an evaluation of a buffer zone strategy for fox control. *Wildlife Research* **27**(5): 465-472. https://doi.org/10.1071/WR99036

Twigg, L. E., Lowe, T. J., Gray, G. S., Martin, G. R., Wheeler, A. G. and Barker, W. 1998. Spotlight counts, site fidelity and migration of European rabbits (*Oryctolagus cuniculus*). *Wildlife Research* **25**(2): 113-122. https://doi.org/10.1071/WR97065

Wallach, A. D., Murray, B. R. and O'Neill, A. J. 2009. Can threatened species survive where the top predator is absent? *Biological Conservation* **142**(1): 43-52. DOI: 10.1016/j.biocon.2008.09.021

Westbrooke, M. E., Florentine, S. K. and Milberg, P. 2005. Arid land vegetation dynamics after a rare flooding event: influence of fire and grazing. *Journal of Arid Environments* **61**(2): 249-260. DOI: 10.1016/j.jaridenv.2004.09.004

Whitehouse, S. J. O. 1977. Movements of dingoes in Western Australia. *Journal of Wildlife Management* **41**(3): 575-576. DOI: 10.2307/3800532

Wood, D. H. 1980. Demography of a rabbit population in an arid region of New South Wales Australia. *Journal of Animal Ecology* **49**(1): 55-79. DOI: 10.2307/4277

Yarnell, R. W., Scott, D. M., Chimimba, C. T. and Metcalfe, D. J. 2007. Untangling the roles of fire, grazing and rainfall on small mammal communities in grassland ecosystems. *Oecologia* **154**(2): 387-402. DOI: 10.1007/s00442-007-0841-9

Downloaded from http://meridian.allenpress.com/australian-zoologist/article-pdf/41/3/417/3125756/i0067-2238-41-3-417.pdf by guest on 13 March 2024